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Foraging Ecology and Fisheries Interactions of Common Bottlenose Dolphins (*Tursiops truncatus*) Inferred From Strandings in Western Iberian Atlantic Waters

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ABSTRACT

The common bottlenose dolphin (*Tursiops truncatus*) is a resident species along the Portuguese mainland coast, yet knowledge of its stranding patterns and feeding ecology is scarce. This study presents a comprehensive assessment of strandings ($n = 264$, from 1980 to 2019) and feeding ecology based on stomach content analysis ($n = 43$ from 1997 to 2019) along the Portuguese mainland coast. Strandings were more frequent in the first half of the year and have increased in recent decades, particularly along the northwestern and southern coasts, likely reflecting improved monitoring efforts. Dietary analysis revealed a predominantly piscivorous diet ($> 85\%$ by number and weight), with prey including pelagic, meso-pelagic, and demersal fish species. Hake (*Merluccius merluccius*), conger eel (*Conger conger*), and blue whiting (*Micromesistius poutassou*) emerged as the most important prey items. Despite a preference for demersal and mesopelagic fish, dolphins exhibited dietary plasticity, foraging across diverse habitats, likely adapting to local prey availability. The substantial dietary overlap with commercially targeted species, particularly by small-scale and coastal fisheries, suggests potential interactions and competition for shared resources. These findings provide valuable insights into the trophic ecological role of bottlenose dolphins in the region and highlight the need to consider this species in ecosystem-based fisheries management and conservation planning.

1 | Introduction

The common bottlenose dolphin, *Tursiops truncatus*, Montagu 1821, (hereafter referred to as bottlenose dolphin) is a widely distributed cetacean species, inhabiting temperate to tropical marine environments and adapting to different habitats from marine to estuarine or even ranging into rivers. The species is primarily coastal, although pelagic/offshore ecotypes have also been documented, each characterized by distinct morphological, ecological, and physiological adaptations (Connor et al. 2000; Wells and Scott 2008). In European waters, bottlenose dolphins are protected under the Habitats Directive (92/43/EEC) and are listed in Annexes II and IV. Their inclusion in Annex II requires member states to designate Special Areas of Conservation (SACs) to ensure the protection of their populations.

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As top predators, bottlenose dolphins play an important role in marine ecosystems, and understanding their trophic ecology is essential for ecosystem-based management. However, studying the diet and ecological interactions of free-ranging cetaceans remains challenging. In this context, stranded individuals provide a valuable source of biological information, allowing the assessment of diet, life-history traits, and causes of mortality and offering key insights into population status and interactions with anthropogenic activities, particularly fisheries (Marçalo et al. 2018, 2021; Peltier et al. 2012; Saavedra et al. 2017).

In the north-east Atlantic, bottlenose dolphins occur along the coasts of the United Kingdom, Ireland, France, Spain, and Portugal, displaying patchy distributions that often reflect discrete coastal and offshore populations (Hammond et al. 2017; Gilles et al. 2023). Along the Iberian Atlantic coast, bottlenose dolphin populations are predominantly coastal, with two well studied resident groups identified in the Sado Estuary (Portugal) and in Galician waters (northwest Spain) (Methion and López 2018; Methion and Díaz López 2019; Santos, Coniglione, and Louro 2007). Recent abundance and distribution surveys have further confirmed this coastal distribution pattern (Gilles et al. 2023). Moreover, the species is widely reported to interact with coastal fisheries mainly by depredation in bottom set-net fisheries along the Southern Portuguese mainland coast (Marçalo et al. 2024, 2025) and across the adjacent Mediterranean waters (Snape et al. 2018), and aquaculture facilities in Galicia (Methion and López 2018; Methion and Díaz López 2019). Such coastal preferences may increase exposure to anthropogenic pressures such as pollution and fisheries-related mortality (Marçalo et al. 2024, 2025; Monteiro et al. 2016), highlighting the need for long-term monitoring and robust conservation strategies.

Bottlenose dolphins regularly occur in waters off western Iberia, where sightings and strandings occur in Spain (Galicia and Gulf of Cadiz) (López et al. 2002; Giménez et al. 2017), as well as in mainland Portugal (Vingada and Eira 2018; Hofman et al. 2026). In Galicia, the species is the second most frequently stranded cetacean (López et al. 2002) and among the most frequently observed (López et al. 2004; Pierce et al. 2010). In Portuguese mainland waters, bottlenose dolphin occurrence is known from historical data (Brito and Sousa 2011), as well as from sightings based on interviews and visual surveys (Alexandre et al. 2022; Brito et al. 2009; Goetz et al. 2015; Vingada and Eira 2018) and recent analysis of cetacean strandings along the southern coast (Algarve) (Hofman et al. 2026). Additional information comes from behavior and bioacoustic studies of the resident population in the Sado River Estuary (Luís et al. 2016; Santos et al. 2005; Santos, Coniglione, and Louro 2007), inferences on contaminants (Monteiro et al. 2016), and diet from a few animals stranded in the southern coast (Algarve), included in a study from the Gulf of Cadiz (Giménez et al. 2017).

In European waters, the diet of bottlenose dolphins has been studied via stomach content analysis (SCA) and stable isotope analysis (SIA), showing that the species is a generalist predator. Prey typically includes demersal and benthopelagic fishes such as European hake (*Merluccius merluccius*), conger eel (*Conger conger*), red mullet (*Mullus* spp.), gadoids such as blue whiting (*Micromesistius poutassou*), saithe, pollock (*Pollachius* spp.), and haddock (*Melanogrammus aeglefinus*), as well as cephalopods such as *Sepia officinalis* and *Octopus vulgaris* (Blanco et al. 2001; Giménez et al. 2017; Hernandez-Milian et al. 2015; Santos et al. 2001; Santos, Fernández, et al. 2007; Spitz et al. 2006). In the Gulf of Cadiz, bottlenose dolphins predominantly ingested conger eel and hake (Giménez et al. 2017), while assimilated diet based on stable isotopes revealed a greater contribution from Sparidae and mackerels. These complementary techniques underscore the importance of combining methods to fully understand trophic ecology. Moreover, the species is adept at exploiting human-influenced food sources, such as discards or bycatch (Bearzi et al. 2008; Brotons et al. 2008; López 2006; Marçalo et al. 2024; Snape et al. 2018), which may influence foraging patterns and dietary profiles, especially in areas of high fisheries productivity or discarding practices.

Despite these advances, studies combining information from stranded individuals to investigate both feeding ecology and fisheries interactions of bottlenose dolphins along the Portuguese mainland coast remain limited. Anthropogenic pressures are high along the entire Portuguese mainland coast due to coastal fishing activities (Alexandre et al. 2022; Marçalo et al. 2024; Vingada and Eira 2018; Hofman et al. 2026) and tourism (Silva et al. 2024). For instance, depredation of bottom-set nets by bottlenose dolphins on the southern coast has raised growing concerns (Marçalo et al. 2024, 2025). Monitoring the potential impacts of these activities on cetaceans is essential to assess their severity and potential consequences for dolphin populations. Furthermore, as cetaceans are major consumers within marine food webs (Bowen 1997), analysis of stranded individuals can provide important population metrics (e.g., diet, life history, causes of death), which can be a major contribution to understanding the health status and trophic role of the populations and their interaction with fishing activities (Marçalo et al. 2021; Peltier et al. 2012; Saavedra et al. 2017).

In this study, we used stranded bottlenose dolphins to investigate foraging ecology and fisheries interactions along the Portuguese mainland coast. Specifically, we analyzed strandings data (1980–2019) and diet composition (1997–2019), described spatial and seasonal patterns, assessed potential causes of mortality, and examined diet through stomach content analysis, considering both intrinsic (e.g., sex, body size) and extrinsic (e.g., location, season) variables. Our goal was to provide updated baseline data on bottlenose dolphin feeding ecology and to explore possible overlaps with fisheries, ultimately contributing to ecosystem-based management and conservation of the species in the region.

2 | Materials and Methods

2.1 | Study Area

During 1980 to 2019, bottlenose dolphin strandings were recorded along mainland Portugal. For spatial analysis, the coastline was divided into three areas based on different topographical and oceanographical conditions, following previous studies (Nicolau et al. 2016; Marçalo et al. 2021) (Figure 1).

The North–Central (NC) region, extending from Caminha to Peniche, is characterized by a wide continental shelf and strong,

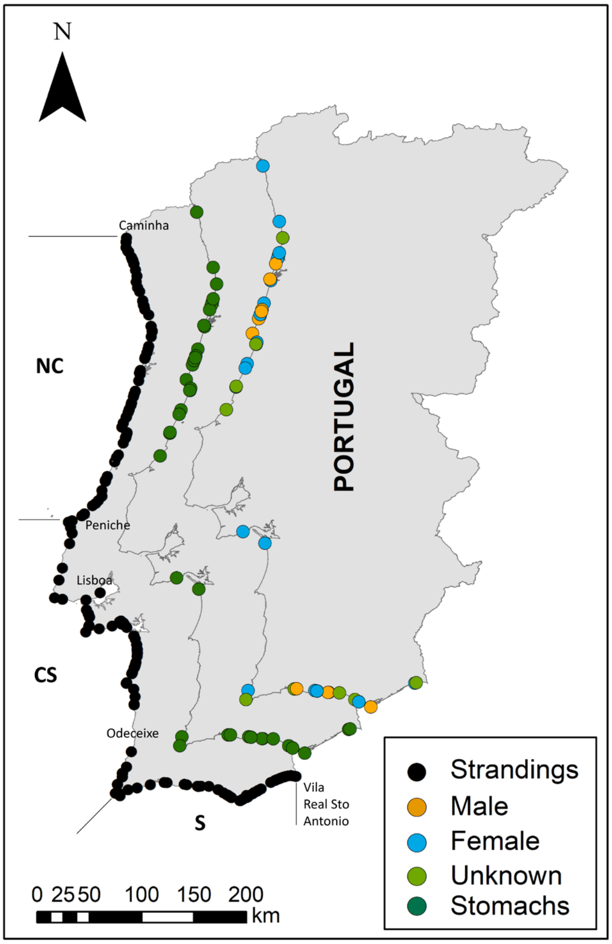

FIGURE 1 | Stranding locations of bottlenose dolphin along the Portuguese mainland coast (1980–2019). Land is represented in gray and ocean in white. Black dots indicate all recorded strandings. Colored dots represent a subset of stranded individuals for which additional biological information was available: Dark green = stomach contents analyzed; orange = male; blue = female; light green = unknown sex. All strandings are shown along the coastline. The coast was divided into three regions: North–Central western coast (NC), Central–Southwestern coast (CS), and southern Algarve coast (S).

persistent upwelling associated with northerly winds, resulting in high productivity. The Central–South (CS) region, from Peniche to Cabo de São Vicente, has a narrower shelf, more heterogeneous coastal morphology, and weaker upwelling influenced by submarine canyons, leading to comparatively lower productivity. The South (S) region (Algarve coast), from Cabo de São Vicente to Vila Real de Santo António, is characterized by a very narrow continental shelf, warmer waters, and predominantly southerly wind regimes.

2.2 | Sample Collection

Dedicated local stranding teams, maritime authorities, or protected areas staff record strandings of bottlenose dolphins as part of the National strandings network, coordinated by the Institute of Conservation of Nature and Forests (ICNF) (see Marçalo et al. 2021 for more details). When dedicated effort occurred, detailed necropsies were performed by trained technicians/biologists and the cause of stranding was determined based on full external and internal examination (Geraci and Lounsbury 2005). Cause of death was only determined when strandeds individuals were found fresh or in a moderate decomposition stage (≤ 3 stages) since an advanced decomposition state may mask evidence of the cause of death (Geraci and Lounsbury 2005). Classification of cause of death used was: (1) by-catch (evidence of unequivocal signs of interactions with fisheries such as presence of netting and/or net marks on the body surface and anterior margins of flippers and fins; amputations of the fins or tail/peduncule), (2) probable by-catch (attributed to animals up to moderate decomposition preventing establishment of other possible causes, but which had good nutritional status, intact prey in the esophagus and/or abundant stomach contents, suggesting recent feeding; Marçalo et al. 2018, 2021), (3) boat collision (attributed to propeller marks), (4) disease, and (5) not determined (all individuals for which the cause of death was not determined at the time of the necropsy). In areas where no local stranding teams operated, only basic data (biometric, species identification and sex) were recorded. With these strandings, the cause of death (when indicated) was based solely on external observations of the carcass (e.g., presence of nets, cables, or hooks, cuts due to bycatch or boat collision, lesions indicative of anthropogenic interaction of some sort).

Diet samples were obtained from 43 stomachs (10 females, 22 males and 11 unknown-sex animals; Figure 1), available from 2002 to 2019 in the NC area ($N = 25$), 1997–1998 in the CS area ($N = 2$), and 2010–2016 in the S area ($N = 16$). Whole stomachs were removed and stored at −20°C in polyethylene bags until further analysis.

2.3 | Stranding Analysis

Temporal (monthly, seasonally, and annually) and spatial trends in strandings were assessed. Bottlenose dolphin size distributions and cause of death were investigated for the overall study period due to limited sample sizes when subdividing the data temporally. To allow for comparisons between areas having different coastal shoreline lengths, relative stranding densities were estimated as the number of strandings per 10 km and calculated for each coastal segment, which constituted the unit of analysis in statistical tests. The earlier years (1980–1989) contained a smaller number of records for the entire Portuguese coastline. Thus, low annual sample sizes could reduce the ability to detect temporal patterns (type II errors) (Quinn and Keough 2002). Following previous approaches (Marçalo et al. 2021; Nicolau et al. 2016), strandings were aggregated into a first period of 10 years (1980–1989) followed by 5-year periods from 1990 to 2019, to improve statistical robustness and allow for temporal comparisons. Seasons were defined as follows: winter–January to March; spring—April to June; summer—July to September; and autumn—October to December. Stranding densities (spatial, seasonal, and annual) were analyzed using nonparametric tests (Kruskal–Wallis and post hoc Dunn's test) because the assumptions of normality (Shapiro–Wilk test) and homoscedasticity (Equal Variance Test) were not fulfilled in some time periods or areas even after data transformation. The maps were generated using ArcMap 10.7.1.

Bottlenose dolphins were classified into two size-based maturity classes following Sergeant et al. (1973), who reported sexual maturity at approximately 235 cm for females and 245 cm for males. However, as no individuals in our dataset fell within the intermediate range (235–245 cm), applying a single threshold of 235 cm did not result in any misclassification. Therefore, for consistency across all individuals, including those of unknown sex, a threshold of 235 cm was applied. Individuals ≤ 235 cm were classified as calves/juveniles/sub-adults, and those >235 cm as adults. Lengths of male and female dolphins were compared using the Kruskal–Wallis nonparametric test using the stats package in R (R Core Team 2021) because the assumptions of normality (Shapiro–Wilk test) and homoscedasticity (Equal Variance Test) were not fulfilled.

2.4 | Diet Analysis

2.4.1 | Prey Identification and Size

At the time of analysis, the stomach contents were thawed and subsequently washed, and diagnostic parts (i.e., fish bones, sagittal otoliths and cephalopod beaks) were treated and stored following Marçalo et al. (2018, 2021). They were later identified to the lowest possible taxonomic level using published guides (Clarke 1986; Härkönen 1986; Tuset et al. 2008) and reference collections compiled from locally collected fish and cephalopod specimens from the Portuguese coast. The minimum number of fish of each species/taxon was determined as half the highest number of paired structures (i.e., sagittal otoliths, opercula, dentaries, maxillae, or premaxillae). The number of upper or lower beaks, whichever was higher, was used for cephalopods. Diagnostic hard parts were measured to the nearest 0.02 mm under a binocular microscope fitted with a digital eyepiece probe following established standards (Clarke 1986; Härkönen 1986). Only undamaged (unbroken and not obviously eroded) otoliths were used to avoid errors associated with reduction in otolith size due to erosion by stomach gastric acids. In addition, reconstructed prey sizes were checked for biological plausibility to ensure that no unrealistic estimates were retained. When there were more than 30 diagnostic remains in a sample, a random subsample of 30 was measured. Individual prey body length and mass were calculated using regressions described in published literature (Supporting Information; Clarke 1986; Tollit et al. 2010; Giménez et al. 2016, 2017; Marçalo et al. 2018, 2021).

2.4.2 | Dietary Variation

The relative importance of each prey type in the diet in terms of presence/absence, number and estimated weight was expressed as the percentage of occurrence (%O, i.e., number of stomachs where prey taxon *i* was found divided by the total number of stomachs), percentage of the total number of prey (%N, i.e., numerical percentage of each prey taxon *i* in relation to the total number of prey individuals found in the stomachs) and the percentage of total prey weight (%W, i.e., the percentage of total reconstructed prey biomass which comprised prey taxon *i*). The Index of Relative Importance ($\text{IRI} = (\%\text{N} + \%\text{W}) \times \%\text{O}$) was also computed as a summary index of dietary composition (Hyslop 1980).

Confidence limits for diet composition, taking into account sampling error, were calculated by bootstrapping for overall %N, %O, %W, and IRI. The procedure involves the addition of all prey numbers or weights from a sample to the total diet each time a sample is selected. When *n* samples were taken, numbers or weights for each prey category were expressed as percentages of the all-categories total and the results were stored. One thousand runs were performed and the median and 95% confidence limits were calculated. The bootstrap routine was written using R 4.1.0 (R Core Team 2021).

Dolphin diet variability was characterized graphically using the Costello diagram (Costello 1990, modified by Amundsen et al. (1996)), in which prey-specific importance of each prey taxon (%P, Equation 1) is plotted against frequency of occurrence (%O):

$$\% P_i = \left(\frac{\sum_i W_i}{\sum_{ti} W_{ti}} \right) \times 100 \tag{1}$$

where W_i is the contribution by weight of prey taxon *i* to the stomach contents, and W_{ti} is the total stomach contents weight for those individual predators with prey taxon *i* in their stomachs. The position of prey types within the diagram provides information on the relative importance of prey, predator feeding strategy, and niche width (Amundsen et al. 1996; please refer to the scheme in Figure 5 for visual support). The diet was characterized using the overall sample ($N=43$) and also for the most represented areas, NC ($N=25$) and S ($N=16$).

The number of prey types (prey diversity) variation with dolphin length was studied using a Generalized Additive Model (GAM) with a negative binomial family distribution for over-dispersed count data. A Generalized Additive Mixed Model (GAMM) with a negative binomial distribution, where dolphin ID was included as a random factor, was used to investigate the prey length versus dolphin length relationship. Both models were checked to ensure normality and any obvious patterns in the residuals. Statistical analyses were performed using the stats package (R Core Team 2021) and the mgcv package (Wood 2004). Results were plotted using the ggplot2 package (Wickham 2009) in R 4.1.0 (R Core Team 2021).

3 | Results

3.1 | Trends in Stranding Records

Between 1980 and 2019, a total of 264 bottlenose dolphins was reported stranded along the Portugues e coastline. Strandings were observed across the entire coast, with the North-Central (NC), Central-South (CS), and South (S) areas accounting for 20.1% ($N=53$), 52.3% ($N=138$), and 27.6% ($N=73$) of the records, respectively. Up to 2009, the Central-South (CS) area accounted for the highest number of strandings. However, from 2010 onwards, a marked increase was observed in the NC and S areas, with the S area showing the most pronounced rise (Figure 2A). When analyzing strandings per km of coastline (Figure 2B), the highest rates were recorded in the CS and S areas during 1995–1999.

Strandings were recorded year-round for both female and male bottlenose dolphins with a higher frequency of events recorded

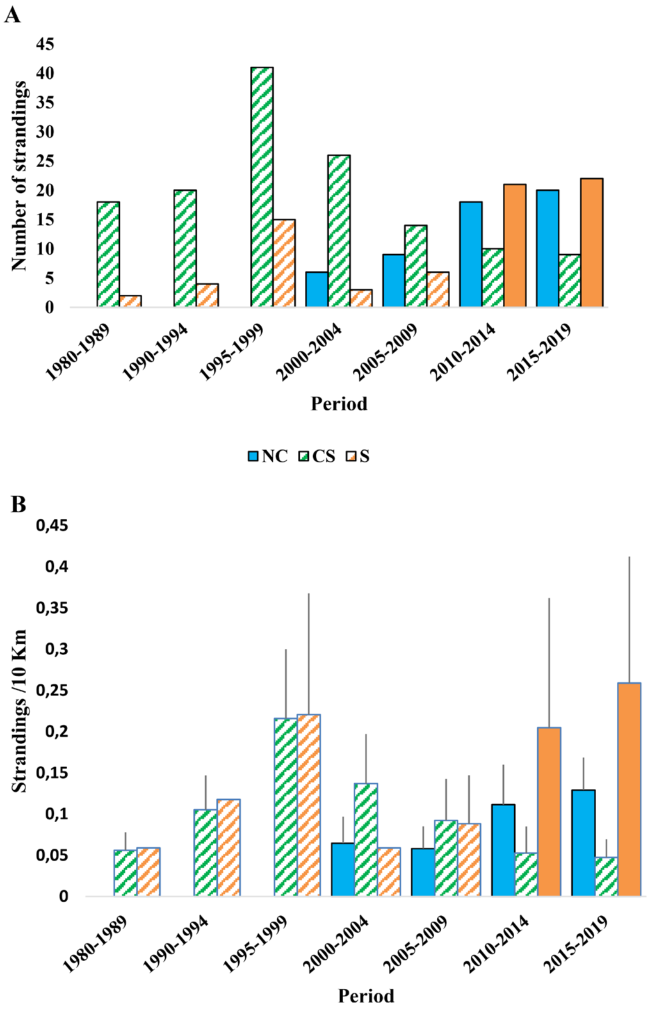

FIGURE 2 | Annual bottlenose dolphin stranding densities in each area: (A) Total number of strandings; (B) Relative density (number of strandings per 10 km with standard error). Columns with full colors refer to areas with dedicated regional stranding networks; Columns with striped colors refer to areas with no dedicated regional stranding networks. Blue-NC; Green-CS; Orange-S.

during the first half of the year, accounting for 56.8% of all records. March, April, and August were the months with the highest number of strandings, representing 34.8% of the total (Figure 3A). Live strandings ($N = 9$) occurred throughout the year in all areas, with a peak during spring ($N = 5$). Sex was determined for 149 dolphins, with 90 males and 59 females identified.

Relative stranding density varied significantly across time periods (Kruskal–Wallis test, $H_6 = 18.02$ $p < 0.05$). For this analysis, the unit of observation was the relative stranding density calculated for each 10 km coastal segment within each time period. Pairwise comparisons revealed significantly fewer strandings during 1980–1989 and 2005–2009 compared to the peak period of 1995–1999 (Dunn's test, all comparisons $p < 0.05$). Relative stranding density, differed significantly among sectors, with higher values in the S area compared to the NC and CS areas (Kruskal–Wallis test, $H_2 = 17.13$ $p < 0.001$). No significant seasonal differences were found in overall or area-specific relative stranding densities (Kruskal–Wallis test, $H_3 = 3.52$ $p = 0.32$).

Total lengths were available for 192 dolphins (Figure 3B), ranging from 112 to 430 cm, with a mean of 263.9 (SD ±63.8 cm). Of these, 47% were males, 31% were females, and 22% were of unknown sex. Juveniles and subadults (total length < 235 cm) accounted for 27.6% of the sample ($N = 53$; 21 males, 19 females, and 13 of unknown sex), while adults (> 235 cm) comprised 72.4% ($N = 139$; 69 males, 40 females, and 30 of unknown sex). No significant differences in mean total lengths were observed between sexes (Females: $N = 59$; mean ± SD = 254.9 ± 67.2 cm; Males: $N = 90$; mean ± SD = 271.2 ± 64.9 cm; Kruskal–Wallis test, $H_1 = 1.74$, $p = 0.187$).

Cause of death was investigated for 67 dolphins among the whole dataset (1980–2019), from which 40 were from 2000 onwards (60%; the period when dedicated local stranding networks were operating). From 1980 to 2019, causes of death were determined for 38 animals, while 29 cases remained undetermined due to inconclusive necropsies. Anthropogenic interactions accounted for 82% of the cases with identified causes, with interactions with fisheries being the predominant cause ($N = 26$; Figure 3C). When local stranding networks were operating, namely from 2000 in the northwestern coast and from 2010 in the southern coast, causes of death were determined for 27 animals, while 13 cases remained undetermined due to inconclusive necropsies. Anthropogenic interactions accounted for 85% of the cases with identified causes, with interactions with fisheries being the predominant cause ($N = 19$; Figure 3D).

3.2 | Diet Analysis

Forty-three stomachs were analyzed, and the remains of 3077 individual fish, 101 cephalopods, and 349 crustaceans, corresponding to a total reconstructed prey biomass of about 509 kg (an average of approximately 12 kg per stomach) were identified. We identified 42 fish taxa, seven cephalopod taxa, and at least four crustacean taxa, belonging to 36 families, using fish otoliths and bones, cephalopod lower and upper beaks, and carapace remains and shells for crustaceans, with 89.0% of all prey items identified to at least genus level (Table 1; check Supporting Information for complete table).

The diet of bottlenose dolphins consisted mainly of fish (86.8%N; 95.4%O; 89.0%W; 16, 767.4 IRI), and to a lesser extent of cephalopods (2.9%N; 48.8%O; 11.0%W; 674.9 IRI). Remains of crustaceans were present in seven stomachs, but most likely were a result of secondary ingestion (remains of prey from the prey). Overall, and as indicated by the IRI index and also numerical importance (%N), Merlucciidae (hake), Congridae (conger eel) and Gadidae (blue whiting), stand out as the most important prey categories.

By percentage of occurrence (%O), hake, closely followed by conger eel, and the families Gadidae (blue whiting, pout; *Trisopterus* spp.), Carangidae (scads, *Trachurus* spp.), and Octopodidae (common octopus, *Octopus vulgaris*), were the most frequently occurring prey. In reconstructed weight (%W), the family Mugilidae (mullets, *Chelon* spp.), which was only present in nine stomachs, was the most important prey, followed by hake, conger eel, common octopus (present in only 11 stomachs), and blue whiting. Reconstructed prey lengths ranged between 11 and 1165 mm (Figure 4).

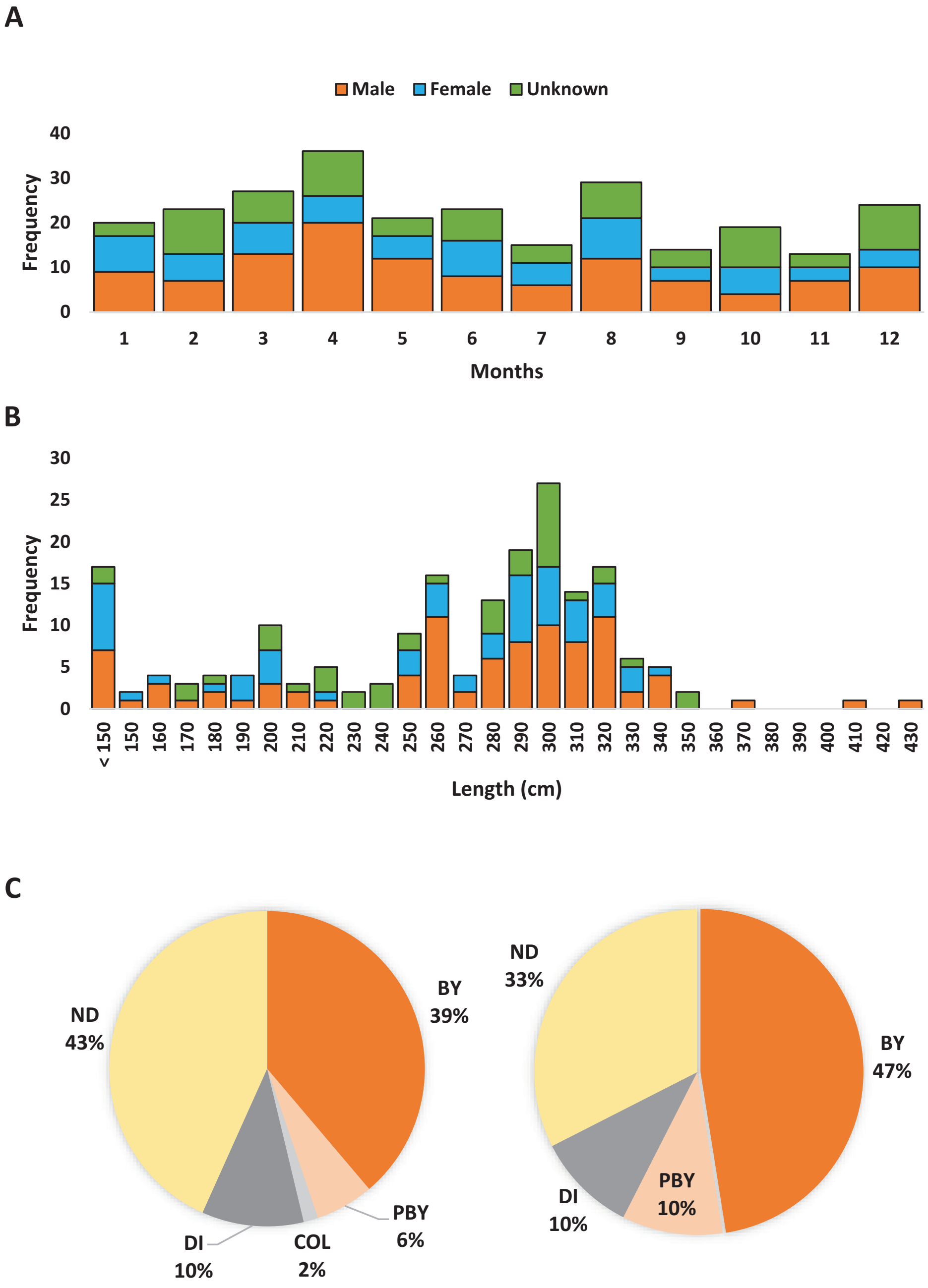

FIGURE 3 | Stranding patterns and cause of death of bottlenose dolphins along mainland Portugal (1980–2019). (A) Stranding monthly distribution ($N = 264$); (B) Length distribution ($N = 149$); (C) Causes of death by percentage of assessed bottlenose dolphins (1980–2019) with decomposition state ≤ 3 ($N = 67$); (D) Causes of death by percentage of assessed bottlenose dolphins (2000–2019) with decomposition state ≤ 3 when local stranding networks of NC (2000–2019) and S (2010–2019) were operating ($N = 40$). BY, bycatch; COL, collision; DI, disease; ND, not determined; PBY, probable bycatch.

Smaller prey (11–100 mm) were mainly composed of fish such as *Gobiidae* spp., *Gadidae* spp. (pouts, *Gadiculus argenteus* and *Trisopterus* spp.), small hakes, blue whiting, and conger eels, and also the benthopelagic fish *Nezumia aequalis*, as well as cephalopods such as small *Loligo vulgaris*, *Sepia* spp., *Todarodes* spp., and *Eledone cirrhosa*. The most important prey above 100 mm in length were conger eel, hake, blue whiting, and mullets. The largest prey items (above 700 mm) found were conger eel (734.1–1165.1 mm).

The modified Costello diagram (Figure 5) suggests that bottlenose dolphins along the Portuguese mainland coast showed varying degrees of specialization and generalization on different prey items. They displayed a mixed diet, but there are three pivotal prey species in occurrence (hake, conger eel, and blue whiting) with spatial variations. For instance, in both areas (NC and S areas), hake and conger eel are favored, but blue whiting stands out in the NC area only, and common octopus and *Chelon* spp. are more important in the south. We could find prey species positioned in the lower left corner (< 50% of prey-specific abundance, < 50% of frequency), characteristic of "rare" species with low occurrence and low specific importance, and species with higher specific importance

TABLE 1 | Diet composition of bottlenose dolphins in Portuguese mainland waters (prey with equal or more than 10 items recorded).

Family	Species	*N*	%N	O	%O	W	%W	IRI
Merlucciidae	*Merluccius merluccius*	562	15.86 [8.51–25.40]	26	60.47 [46.51–74.42]	112098.73	22.01 [12.05–36.36]	2290.21 [956.42–4596.19]
Congridae	*Conger conger*	445	12.56 [7.50–19.74]	25	58.14 [44.19–72.09]	72014.80	14.14 [8.46–20.98]	1552.47 [705.09–2935.94]
Gadidae	*Micromesistius poutassou*	710	20.04 [6.54–35.73]	14	32.56 [18.60–46.51]	46620.53	9.16 [1.79–21.13]	950.53 [155.04–2644.98]
	Trisopterus spp.	62	1.75 [0.88–3.01]	14	32.56 [18.60–46.51]	3143.80	0.62 [0.27–1.18]	77.08 [21.36–194.59]
	Gadiculus argenteus	16	0.45 [0.10–1.01]	5	11.63 [2.33–20.93]	92.41	0.02 [0–0.04]	5.46 [0.24–22.09]
Mugilidae	*Chelon* spp.	109	3.06 [0.97–6.33]	9	20.93 [9.30–32.56]	148074.00	29.08 [10.70–44.17]	673.03 [108.51–1644.28]
Carangidae	*Trachurus* spp.	159	4.49 [0.91–10.98]	14	32.56 [18.60–48.84]	9779.04	1.92 [0.44–4.43]	208.64 [25.02–752.20]
Cepolidae	*Cepola macrophthalma*	314	8.86 [0.14–19.12]	6	13.95 [4.65–25.58]	7977.06	1.57 [0.01–4.17]	145.52 [0.72–595.64]
Centriscidae	*Macroramphosus* spp.	177	5 [0–14.45]	2	4.65 [0–11.63]			
Scombridae	*Scomber colias*	60	1.69 [0.27–3.86]	8	18.60 [6.98–30.23]	5786.00	1.14 [0.33–2.29]	52.65 [4.22–186.10]
	Scomber scombrus	22	0.62 [0.05–1.42]	5	11.63 [2.33–20.93]	3290.61	0.65 [0.06–1.49]	14.73 [0.26–61.10]
Sparidae	*Boops boops*	45	1.27 [0.15–3.08]	7	16.28 [6.98–27.91]	2644.61	0.52 [0.08–1.29]	29.13 [1.61–122.08]
	Diplodus spp.	18	0.51 [0.03–1.54]	4	9.30 [2.33–18.60]	4289.11	0.84 [0.01–2.57]	12.56 [0.09–76.47]
	Pagellus acarne	13	0.37 [0–1.01]	2	4.65 [0–11.63]	1160.17	0.23 [0–0.63]	2.77 [0–19.11]
	Pagellus erythrinus	17	0.48 [0–1.37]	3	6.98 [0–16.28]	1118.74	0.22 [0–0.69]	4.88 [0–28.69]
	Sparidae spp.	27	0.76 [0.11–1.66]	6	13.95 [4.65–25.58]			
Triglidae	*Aspitrigla cuculus*	73	2.06 [0–7.47]	2	4.65 [0–11.63]	4775.04	0.94 [0–3.65]	13.94 [0–129.24]
	Triglidae spp.	33	0.93 [0.25–1.89]	9	20.93 [9.30–32.56]	1748.75	0.34 [0.08–0.74]	26.68 [3.05–85.51]
	Chelidonichthys gurnardus	13	0.37 [0–1.29]	1	2.33 [0–6.98]	768.08	0.15 [0–0.53]	1.2 [0–12.69]
Clupeidae	*Sardina pilchardus*	22	0.62 [0.10–1.47]	7	16.28 [6.98–27.91]	1524.97	0.30 [0.05–0.74]	14.98 [1.08–61.73]
Soleidae	*Solea senegalensis*	18	0.51 [0–1.64]	3	6.98 [0–16.28]	5977.93	1.17 [0–3.32]	11.73 [0–80.74]
	Solea spp.	12	0.34 [0.05–0.78]	5	11.63 [2.33–20.93]	4684.82	0.92 [0.11–2.23]	14.64 [0.38–62.94]
Gobidae	*Gobidae* spp.	15	0.42 [0.06–1.06]	6	13.95 [4.65–25.58]	58.03	0.01 [0–0.03]	6.07 [0.30–27.67]
Callionymidae	*Callionymus lyra*	10	0.28 [0–1.05]	1	2.33 [0–6.98]	1480.60	0.29 [0–1.01]	1.33 [0–14.35]
Total fish		3077	86.85 [68.80–97.71]	41	95.35 [88.37–100]	453,345	89.03 [75.97–97.67]	16769.75 [12793.51–19534.94]
Loliginidae	*Loligo vulgaris*	35	0.99 [0.10–2.22]	6	13.95 [4.65–25.58]	3439.89	0.68 [0.02–1.58]	23.21 [0.54–97.22]

(Continues)

TABLE 1 | (Continued)

Family	Species	N	%N	O	%O	W	%W	IRI
Octopodidae	*Octopus vulgaris*	24	0.68 [0.26–1.37]	11	25.58 [13.95–39.53]	49612.29	9.74 [1.21–23.47]	266.57 [20.57–982.18]
	Eledone cirrhosa	17	0.48 [0.14–0.90]	5	11.63 [2.33–20.93]	2118.67	0.42 [0.07–0.96]	10.42 [0.48–39.01]
Sepiidae	*Sepia* spp.	10	0.28 [0–1]	1	2.33 [0–6.98]	240.45	0.05 [0–0.18]	0.77 [0–8.25]
Total cephalopoda		101	2.85 [1.37–5.27]	21	48.84 [34.88–65.12]	55,857	10.97 [2.42–23.41]	674.93 [132.04–1867.47]
	Caridea	Shrimp NI	343	9.68 [0–29.17]	1		2.33 [0–6.98]	
Total crustacea		349	9.82[0.06–28.00]	7	13.953 [4.65–25.58]			
Total prey		3544	100.00	43	100.00	509,202	100.00	

Note: In parentheses are 95% confidence intervals.
Abbreviations: %N = numerical percentage; %O = percentage of occurrence; %W = percentage of reconstructed weight; IRI = index of relative importance; *N* = number of prey; O = occurrence; W = prey weight (g).

and occurrence in the upper left corner (> 50% of prey specific abundance).

A positive relationship between dolphin length and prey length ($R^2 = 0.024$, $p < 0.01$) was found, with prey length reaching an asymptote around 250 cm of dolphin length (Figure 6A). Similarly, prey diversity increases with dolphin length ($R^2 = 0.105$, $p < 0.05$), reaching an asymptote around 275 cm (Figure 6B).

4 | Discussion

4.1 | Stranding Trends and Causes of Death

The long-term analysis of bottlenose dolphin strandings along the Portuguese coast (1980–2019) reveals spatially and temporally heterogeneous patterns, shaped by a combination of ecological dynamics and anthropogenic pressures. Strandings were recorded year-round, with notable peaks in spring and summer—especially in March, April, and August—suggesting a seasonal signal likely linked to prey availability and reproductive cycles. These patterns are consistent with seasonal reproductive peaks observed in other populations (Wells and Scott 2008) and coincide with periods of intense fisheries activity, making it challenging to distinguish between natural and anthropogenic drivers.

The marked increase in recorded strandings in the North-Central (NC) and Southern (S) area after 2000 and 2010, respectively, coincides with the establishment of dedicated stranding response teams. In the NC area, all strandings occurred from 2000 onwards, likely reflecting improved monitoring efforts following the establishment of a local stranding response team in 2000. Similarly, the increase in strandings in the S area between 2010 and 2019 is attributed to enhanced monitoring efforts as a local network in the area was established in 2010. This trend illustrates how monitoring effort significantly influences perceived stranding rates—a phenomenon also reported in other studies in the area (Marçalo et al. 2021; Nicolau et al. 2016; Torres-Pereira et al. 2023) and other parts of the globe (Gulland et al. 2025). However, this monitoring bias does not negate the ecological significance of the patterns observed. In the S area, the highest relative density of strandings corresponds to the narrowest portion of the continental shelf, a zone with intense small-scale fishing activity and frequent dolphin-fishery interactions (Marçalo et al. 2024, 2025). This overlap increases the likelihood of bycatch and other anthropogenic impacts in this area, particularly given the prevalence of bottom-set nets, which are known to target demersal or mesopelagic (e.g., hake) species, known as bottlenose dolphins' most frequently eaten prey (Bearzi et al. 2011; Brotons et al. 2008; Goetz et al. 2015; Marçalo et al. 2024). Recent evidence from southern Portugal indicates that bottlenose dolphin abundance and age-class distribution are influenced by environmental drivers, particularly sea surface temperature and chlorophyll-a, likely through their effects on prey availability (Vizeu-Pinheiro et al. 2025). These environmental gradients may contribute to spatial differences in dolphin occurrence and vulnerability, and could partially modulate stranding patterns when acting in combination with anthropogenic pressures. Although little is known about the seasonal movements of bottlenose dolphins in this

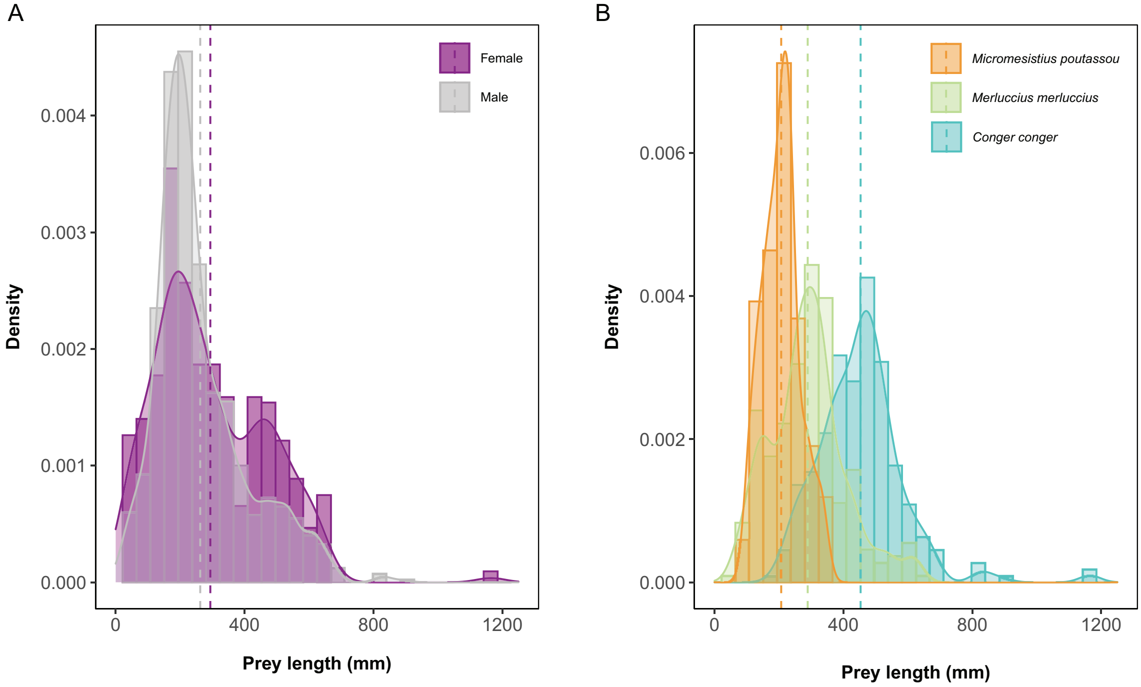

FIGURE 4 | Density distribution of estimated length bottlenose dolphin prey: (A) all prey, for male and female bottlenose dolphins; (B) distribution of three main prey types (Hake, *Merluccius merluccius*; Conger, *Conger conger*; Blue whiting, *Micromesistius poutassou*). Dashed lines represent means.

region, anecdotal reports from fishers and opportunistic observations by local whale-watching companies suggest a pattern of local residency (Silva et al. 2024; Vizeu-Pinheiro et al. 2025)—a behavior commonly documented in other populations of this species worldwide (Wells and Scott 2008). The predominance of adult individuals among stranded dolphins (72.4%) suggests that this age group may be disproportionately affected, potentially due to their foraging strategies or a higher likelihood of interactions with fishing gear. Anthropogenic interactions were identified as the primary cause of death. Among these, fisheries interactions were the most prevalent, particularly entanglements in bottom-set nets. These findings align with broader concerns about the impact of small-scale fisheries on bottlenose dolphins in the area (Alexandre et al. 2022; Marçalo et al. 2024, 2025; Vingada and Eira 2018).

The high proportion of strandings with undetermined causes of death and cases left unexamined underscores persistent logistical and operational challenges in stranding response efforts. Factors such as advanced decomposition, inaccessible locations, and limited resources hinder the ability to determine mortality causes accurately, especially when permanent local stranding teams were not available. Addressing these barriers is essential for improving our understanding of the drivers behind stranding events and informing conservation strategies. Given these constraints, stranding patterns should be interpreted in conjunction with other data sources—such as at-sea surveys and fisheries observer programs—to refine our understanding of mortality drivers and population pressures. The particularly high stranding density and prevalence of anthropogenic mortality in the southern area position this region as a conservation priority (Marçalo et al. 2024, 2025). Targeted mitigation strategies—such as gear modifications, time-area fishing closures, and stakeholder engagement—should be urgently developed and implemented to reduce risk to local dolphin populations.

In summary, although increased monitoring effort likely contributes to the observed rise in strandings over recent decades, the ecological signal remains clear: bottlenose dolphins in mainland Portugal face high risk from human activities, particularly fisheries, due mainly to their increased vulnerability in areas with frequent and well-documented depredation events (Marçalo et al. 2024, 2025). Effective conservation planning will therefore require spatially explicit strategies that address both existing data gaps and direct anthropogenic threats.

4.2 | Diet Analysis

The dietary patterns observed in bottlenose dolphins along the Portuguese mainland are consistent with prior studies across the northeast Atlantic and the Mediterranean, reinforcing their generalist and opportunistic feeding strategies (Blanco et al. 2001; Giménez et al. 2017; Santos et al. 2001; Santos, Fernández, et al. 2007; Spitz et al. 2006). The analysis of 43 stomach contents revealed a diverse prey spectrum, encompassing 42 fish taxa, seven cephalopod taxa, and at least four crustacean taxa (Table S1), corresponding to a total reconstructed biomass of approximately 509 kg. Fish constituted the bulk of the diet (86.8%N; 95.4%O; 89.0%W; 16, 767.4 IRI), with cephalopods playing a secondary role and crustaceans likely representing secondary predation. Our results confirm that these dolphins predominantly target hake, conger eel, and blue whiting as cornerstone prey—an observation aligned with findings from the Gulf of Cadiz (Giménez et al. 2017) and Galician waters (Santos,

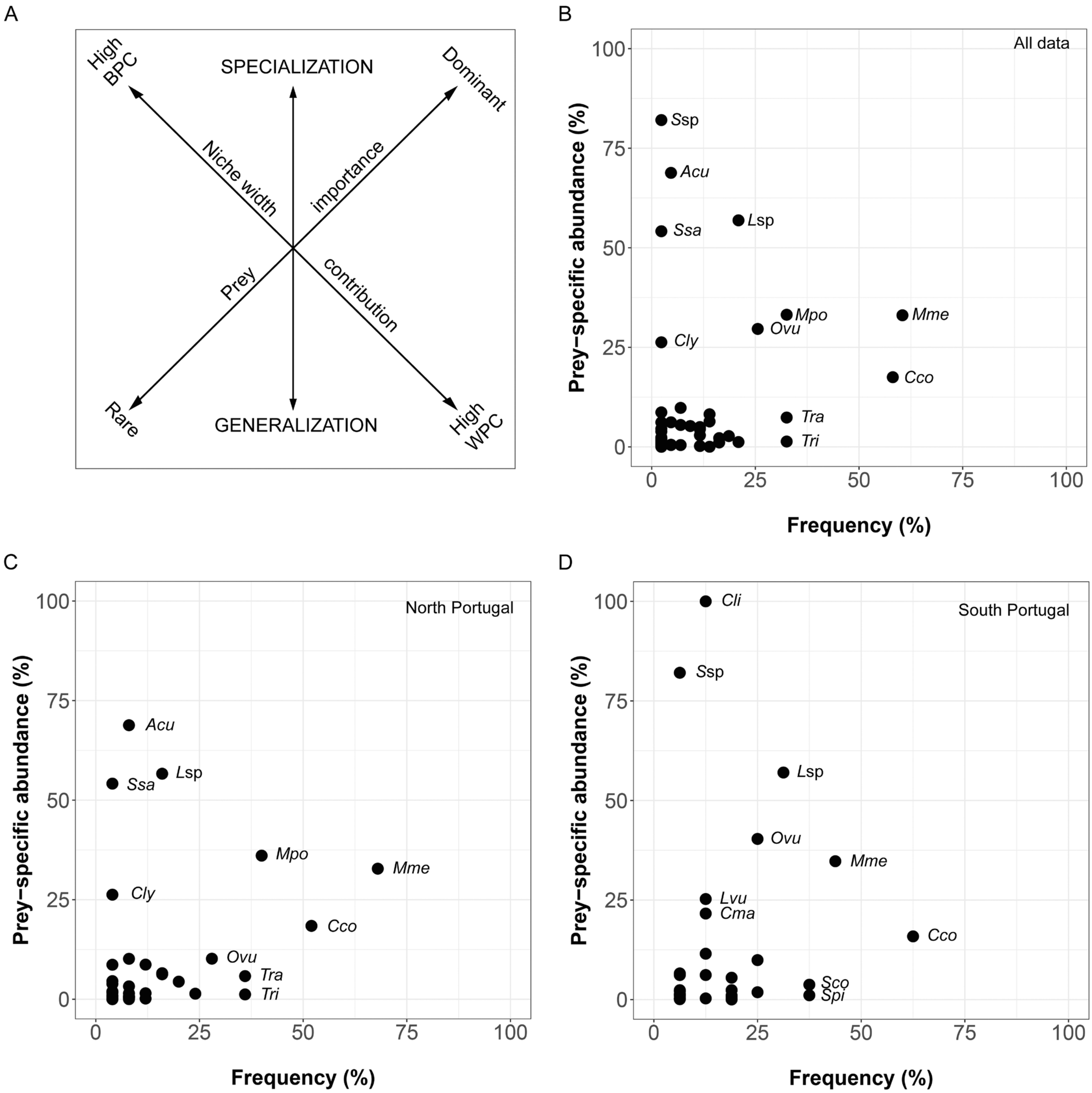

FIGURE 5 | Prey-specific abundance plotted against frequency of occurrence of prey species for common dolphins stranded along the Portuguese mainland coast. (A) Explanatory axes for foraging patterns are those of Costello (1990) as modified from Amundsen et al. (1996). The two diagonal axes represent the importance of prey (dominant vs. rare) and the contribution to the niche width (high between-phenotype contribution (BPC) vs. high within-phenotype contribution (WPC)); the vertical axis defines the predator feeding strategy (specialist vs. generalist). (B) All data; (C) NC area; (D) S area. *Acu*: *Aspitrigla cuculus*; *Cco*: *Conger conger*; *Cli*: *Citharus linguatula*; *Cly*: *Callionymus lyra*; *Cma*: *Cepola macrophthalma*; *Lsp*: *Chelon* spp.; *Lvu*: *Loligo vulgaris*; *Mme*: *Merluccius merluccius*; *Mpo*: *Micromesistius poutassou*; *Ovu*: *Octopus vulgaris*; *Sco*: *Scomber colias*; *Spi*: *Sardina pilchardus*; *Ssa*: *Sarpa salpa*; *Ssp*: *Sepia* spp.; *Tra*: *Trachurus* spp.; *Tri*: *Trisopterus* spp.

Fernández, et al. 2007). The frequency and relative contribution of blue whiting in the Portuguese diet were higher in the western area, while common octopus and *Chelon* spp. gained importance in the south, suggesting geographic variation in the diet. This mirrors findings in Galician waters, where seasonal and spatial variation in prey use was associated with local prey availability (Santos, Fernández, et al. 2007).

The presence of large demersal species, despite their lower frequency of occurrence, contributed disproportionately to the biomass, supporting the idea that largeprey play a vital role in fulfilling the metabolic needs of adult dolphins (Spitz et al. 2006). Furthermore, the significant prey biomass from occasional captures of large conger eels (up to 1165 mm) underscores the energetic payoff of targeting large prey, a trend noted

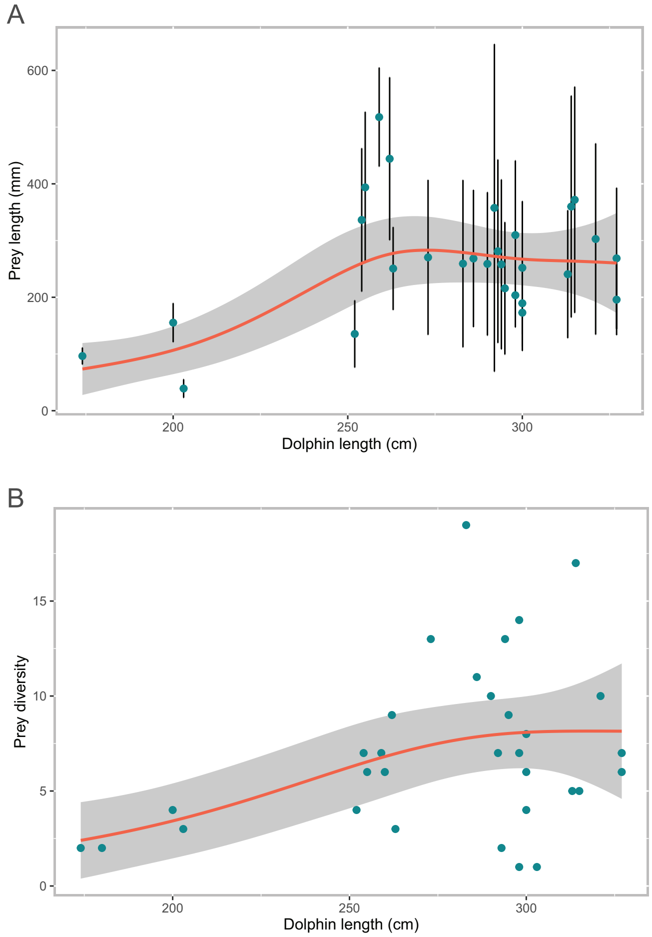

FIGURE 6 | Relationship between dolphin length (cm) and (A) prey length (mm) and (B) prey diversity. Gray shaded area is the 95% confidence interval. Green dots are mean values of each prey lengths consumed by each individual dolphins.

in other regions as well (Blanco et al. 2001; Santos et al. 2001). The absence of certain prey such as *Mullus* spp. (red mullets), despite documented depredation interactions with fisheries targeting this group (Marçalo et al. 2024), may be attributed to selective feeding behavior that avoids ingesting parts necessary for prey identification (e.g., heads with otoliths), as previously described by Lauriano et al. (2004). This limitation emphasizes the need to complement stomach content analysis with other dietary tools like stable isotope or DNA-based methods (Borrell et al. 2020; Giménez et al. 2017).

The reconstructed prey lengths (11–1165 mm) and the positive correlation between dolphin length and prey size indicate ontogenetic shifts in feeding strategies. Larger dolphins (> 250 cm) consume a broader prey size range and exhibit increased dietary diversity, suggesting that size and experience enhance their ability to exploit a wider variety of prey. Prey size asymptotes around 250 cm for length and 275 cm for diversity, aligning with the physical and ecological capabilities of mature individuals.

The modified Costello diagram illustrates the mixed feeding strategy of these dolphins, pointing to a trophic strategy that blends generalist tendencies with specializations—likely driven by local prey abundance and seasonal shifts. This dual strategy has been highlighted in multiple studies as a hallmark of bottlenose dolphins' foraging ecology (Santos, Fernández, et al. 2007; Spitz et al. 2006). While hake, conger eel, and blue whiting dominate as prey, the presence of rare species with low occurrence and specific importance suggests opportunistic feeding on less abundant prey when available. The observed variation in prey specialization across regions further emphasizes the ecological plasticity of bottlenose dolphins.

These findings provide valuable insights into the trophic ecology of bottlenose dolphins in mainland Portugal, highlighting their reliance on key fish species and the influence of regional prey availability. The overlap between their diet and commercially targeted species, such as hake and blue whiting, raises potential concerns about competition with fisheries, particularly in areas where interactions are more frequent, such as the narrow continental shelf of the south coast (Marçalo et al. 2024). Future studies should explore the potential implications of these dietary overlaps for both dolphin conservation and fisheries management.

Moreover, the integration of stranding data with feeding ecology provides valuable insights into the ecological diversity of bottlenose dolphins along the Portuguese coast. While stranding events allow for the collection of biological samples and assessment of general health and threats, they do not enable a clear distinction between individuals from different ecotypes. However, it is well established that both coastal and offshore ecotypes occur in this region (Grave 2022; Correia et al. 2015), each likely exhibiting distinct habitat use and foraging behaviors. Specifically, the occurrence of prey such as red bandfish (*Cepola macrophthalma*) and snipefish (*Macroramphosus* spp.)—non-commercial species often discarded in bottom trawl fisheries operating along the continental shelf (Fernandes et al. 2007)—points to offshore or deeper-water foraging by some dolphins. These findings underscore the importance of coupling dietary data with stranding records to improve our understanding of population structure and to guide more ecotype-specific conservation and management actions.

4.3 | Study Limitations

While this study provides valuable insights into the diet composition and stranding patterns of bottlenose dolphins along the Portuguese mainland, several limitations must be acknowledged. The reliance on stranded individuals for dietary analysis, while practical, inherently introduces potential biases. Stranded animals may disproportionately represent individuals compromised by disease, age, or anthropogenic impacts, and their diet may not fully reflect that of a healthy, free-ranging population, which encompasses a range of health states (Gannon et al. 1997; Marçalo et al. 2018, 2021). Furthermore, while stomach content analysis is effective for identifying recent prey, it has inherent limitations. It may overrepresent prey with hard, durable structures (e.g., otoliths, cephalopod beaks) and underrepresent soft-bodied or rapidly digested prey, potentially skewing the relative importance of different taxa (Tollit et al. 2010). Nevertheless, several studies have found broad dietary consistency between stranded and by-caught individuals (e.g., Santos et al. 2001; Santos, Fernández, et al. 2007), leading support to the use of such data for general trophic assessments (Dunshea et al. 2013).

Additionally, as causes of death for a large share of stranded animals could not be determined, mortality can be considered somewhat biased toward anthropogenic causes. The state of preservation of a cetacean carcass when it reaches the beach is influenced by the time it has been in the water since death, which is related to prevailing currents and the distance from shore where it died. Stranded animals are more likely to include those that died closer to shore, and the proportion of animals in poor preservation state, for which cause of death is difficult to diagnose, will tend to be higher when mortality occurs further offshore. As a result, bycatch mortality may be underestimated when bycatch occurs mainly in offshore waters and overestimated when bycatch occurs inshore. Thus, bycatch rates derived from strandings are difficult to interpret, although this situation may be improved with a better understanding of local current systems, at-sea carcass movements, dolphin and fishery distributions, and the effects of decomposition on cause-of-death diagnosis (Peltier et al. 2012, 2016, 2021).

Spatial and temporal variability in prey availability was not fully addressed due to the limited geographic range and sample size of this study. While the study successfully identified key regional dietary differences, the restricted dataset may not capture the full extent of seasonal or interannual variations in prey composition or abundance. This is particularly relevant in dynamic coastal ecosystems, where environmental and anthropogenic factors can strongly influence prey distribution and availability.

The observed stranding trends provide important context for understanding mortality causes but are constrained by incomplete data on the exact circumstances leading to strandings. For example, it was not always possible to differentiate natural mortality from anthropogenic impacts, such as fisheries interactions or environmental degradation. Additionally, the absence of comprehensive necropsy data for all individuals limits the ability to assess underlying health conditions or cumulative stressors that may contribute to stranding events.

5 | Conclusions

This study provides the most comprehensive assessment to date of common bottlenose dolphin strandings and trophic ecology as represented by diet from stomach contents along the Portuguese mainland, offering important insights into their ecological role and the anthropogenic pressures they face.

The prominence of hake, conger eel, and blue whiting in the diet highlights the species' role as a top predator and its reliance on both demersal and mesopelagic fish—paralleling dietary profiles documented in neighboring waters (Giménez et al. 2017; Santos, Fernández, et al. 2007). Our findings reinforce concerns about the overlap between dolphin foraging grounds and coastal fisheries, which target the same preferred species. This trophic intersection raises the potential for both direct interactions (e.g., bycatch, depredation) and indirect competition for key resources—issues also highlighted in Mediterranean and Atlantic contexts (Blanco et al. 2001; Spitz et al. 2006). Additionally, the observed ontogenetic dietary shifts and regional prey differences further underscore the ecological flexibility of bottlenose dolphins. Such plasticity likely enables them to persist in dynamic and human-impacted environments but may also expose them to increased risk where fisheries pressure is high, such as in the case of the Portuguese mainland coast (López et al. 2002; Marçalo et al. 2024; Silva and Sequeira 2003; Saavedra et al. 2017; Vingada and Eira 2018).

Regarding stranding trends, we identified significant temporal and spatial variations in stranding events, which are likely influenced by both environmental and anthropogenic factors, including fisheries interactions. These findings emphasize the importance of spatially explicit conservation actions to reduce bycatch, particularly in southern Portugal where stranding densities and fisheries overlap are higher.

Finally, our findings provide empirical dietary and spatio-temporal information that can be incorporated into ecosystem and trophic models in which bottlenose dolphins are represented as upper-level predators, thereby supporting ecosystem-based approaches to fisheries management. In particular, the identification of key prey groups and their relative importance contributes to a better understanding of potential trophic overlap with exploited resources, while observed stranding patterns may help identify periods or areas of increased vulnerability. Although our results do not support direct management prescriptions (e.g., gear restrictions or fishing closures), they provide baseline information that can inform risk-based and spatially explicit management frameworks when combined with fisheries effort, bycatch data, and independent monitoring. This contribution is especially relevant in the context of the Marine Strategy Framework Directive (MSFD; 2008/56/EC), which aims to achieve Good Environmental Status of marine waters. By improving our understanding of bottlenose dolphin feeding ecology and associated pressures, this study supports the long-term conservation of the species and the broader functioning of marine ecosystems while acknowledging ongoing human activities.

Author Contributions

Lídia Nicolau: data curation, investigation, writing – review and editing. **Marisa Ferreira:** investigation, data curation, writing – review and editing. **Andreia Torres-Pereira:** writing – review and editing, investigation, data curation. **Ana Marçalo:** conceptualization, investigation, writing – original draft, methodology, validation, visualization, writing – review and editing, formal analysis, data curation. **Catarina Eira:** project administration, funding acquisition, investigation. **Joan Giménez:** conceptualization, formal analysis, methodology, validation, visualization, writing – original draft, writing – review and editing. **Marina Sequeira:** investigation, data curation, writing – review and editing. **Jorge Santos:** investigation, data curation. **Helder Araújo:** investigation, data curation. **Isabel Oliveira:** investigation. **José Vingada:** supervision, investigation, funding acquisition. **Silvia S. Monteiro:** investigation. **Sara Sá:** investigation, data curation. **Maria Casero:** investigation, data curation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Diet composition of common bottlenose dolphins in Portuguese mainland waters. In parentheses are 95% confidence intervals. %N = numerical percentage; %O = percentage of occurrence; %W = percentage of reconstructed weight; IRI = index of relative importance; *N* = number of prey; O = occurrence; W = prey weight.